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Preface

This publication of Professor Bychowsky is a major contribution to the study of the phylogeny of parasitic flatworms. It is a singular coincidence for it to have appeared in print the same year as Stunkard's "The Physiology, Life Cycles and Phylogeny of the Parasitic Flatworms" (Amer. Museum Novitates, No. 908, 27 pp., 1937), and this editor well remembers perusing the latter under the rather demanding tutelage of A.C. Chandler. Bychowsky's paper remained unknown to most parasitologists, however, for many years, and it is largely due to W.J. Hargis, Jr.'s careful husbanding through translation of Bychowsky's monograph on monogenetic trematodes that his earlier work has commanded the interest which it deserves.

In his 1957 work Bychowsky very briefly summarizes the content of his 1937 article and goes on to state (A.I.B.S. translation, W.J. Hargis, Jr., ed., 1961, p. 564), "The views expressed are completely held by us also at the present time." He names several Soviet parasitologists who have accepted his opinions in whole or in part, but also describes at length the objections of D.M. Fedotov.

In truth, Bychowsky's system is not widely used, and apparently has not been widely accepted elsewhere, as a glimpse at any general parasitology text will show. Part I of the 1937 paper is of interest to specialists in monogeneans, principally; Parts II-V are of more general interest. It is not necessary for one to agree fully with any given section, e.g. to accept the basis of his monogene system in full, in order to appreciate the subsequent arguments. It is in the hope of allowing a fair treatment by a larger audience that this translation is given.

The present editor will make a single objection and a proposal and be done with it. This has to do with the taxon, Cercomeromorphae, here given Superclass status by Bychowsky. Not only is the term horribly non-euphonious, but (2) as originally employed by Janicki, it indicated a different concept, and (3) a number of the forms included therein do not possess a cercomer, though, to be sure, they do bear the posterior larval hooks characteristic of this group. Here and now is proposed the name, ONCOPHOREA, for the concept which includes those parasitic flatworms having larvae which develop hooks in a characteristic manner and of a characteristic type, and bear them posteriorly.

The translators have employed the transliteration system of the U.S. Department of Commerce, National Bureau of Standards, Joint Publications Research Service. The editor has changed several names, e.g. Bychowsky, Sinitsin, Janicki, to the spelling which is most familiar to Western readers, and more specifically used by the Index Catalogue of Medical and Veterinary Zoology. Obvious misspellings

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On the basis of studies of the development of monogenetic trematodes, it is possible to establish that their current system is artificial. In this connection, the author attempts to develop a system for monogenetic trematodes not only on the basis of comparative anatomy, but also on the basis of ontogenesis. At the same time, the development of a new system of flatworms is the result of the above propositions.

INTRODUCTION

The purpose of this report is to establish relationship among individual groups of parasitic flatworms, namely, among monogenetic trematodes (Monogenea), digenetic trematodes (Digenea), tapeworms proper (Cestoda), and the so-called Cestodaria group (AMPHILINIDAE and GYROCOTYLIDAE). The attempt to establish the above-mentioned relationships is made to a variable degree for different groups. The main point of this report is the establishment of phylogenetic relationship in the Monogenea, not only for the entire group as a whole, but also for the individual families which are members of this group. We feel that another important point is our attempt at clarifying the phylogenetic position of the GYROCOTYLIDEA group which until very recently has been puzzling in many respects.

On the basis of phylogenetic considerations stated below, we consider it possible to suggest a new system for parasitic flatworms which is essentially different in many respects from the generally accepted current system.

The significance of the solution of these problems lies, undoubtedly, not only in the fact that they shed some light on the obscure points of taxonomy and in the fact that these solutions provide us with a clue for understanding the evolutionary process within the studied group, but also in the fact that these solutions make it possible for us to clarify correctly a number of problems of the biology and development of parasitic flatworms. The solution of the latter is quite often extremely important for answering purely practical questions connected with therapeutic, biological and preventive measures for controlling parasitic worms and diseases caused by them.

Investigations of the phylogeny of lower organisms are hindered greatly by the fact that there is no direct evidence of their evolution, i.e. paleontological remains. This fact makes it necessary

to pay even more attention to the data of comparative anatomy and comparative embryology. However, it should be mentioned here that the embryological evidence of phylogenetic interrelations of parasitic flatworms is not given sufficient attention at the present time. Moreover, as it will be shown further in this paper, embryological materials have not been used at all for monogenetic trematodes.

For parasitic animals, a certain criterion of their phylogenetic relationships, in addition to the above-mentioned ones, can also be aspects of specificity with respect to the host (Fuhrmann's rule for the Cestoda; Bychowsky's rule for the Monogenea) and data on the paleontological antiquity of the host in connection with the parasite's specificity.

However, the utilization of the latter purely "parasitological" criteria of phylogeny is extremely difficult and very often may lead to completely erroneous conclusions, because the rates of the evolutionary processes of the host and of the parasite may be entirely different: a parasite could change considerably more slowly on an extremely rapidly evolving host, or vice versa, which, undoubtedly, will significantly obscure the picture and will hinder the correct utilization of the indicated criteria. It is to be supposed that the presence of a very specialized group as parasites on a definite and very ancient host group still does not permit us to say with a sufficient degree of confidence that the group of parasites is also very ancient. However, such deductions are made quite frequently. As an example, we can cite Fuhrmann's view regarding phylogenetic interrelations within the Subclass Cestoda. Fuhrmann writes: "For establishing the phylogeny of the Cestoda, we have at our disposal the data on the incidence of various orders of the Cestoda among the vertebrates. For example, Tetraphyllidea (with the exception of aberrant PROTOCEPHALIDAE and MONTICELLIDAE), as well as Tetrarhynchidea (exception - one species), live only in selachians. Pseudophyllidea are not present in primitive selachians, but occur in marine teleosts and are common in fresh-water fish and land vertebrates. Cyclophyllidea parasitize only birds and mammals and occur rarely in reptiles and amphibians. On this basis, it is easy to conclude that tapeworms of the most ancient vertebrates (selachians) are the most primitive, and not Pseudophyllidea, as is usually accepted." It should be mentioned here, that in calling Tetraphyllidea "the most primitive", Fuhrmann means that it is equivalent to "the most ancient," which is indicated by the phylogenetic scheme presented by him later. However, this is absolutely inadmissible, because the most ancient forms do not have to be necessarily the most primitive (it seems to us that quite frequently it is just the opposite). The example cited above shows the nature of reasoning when the "parasitological" criteria of phylogeny are applied. The above example as such is not important to us at the present time. Let us only say that Fuhrmann's thesis may even be essentially correct, but the reasons stated by him cannot at all be considered sufficient.

In our deductions, we are using all possible types of evidence of phylogenetic interrelations for the animals which are of interest to us; however, their significance is evaluated differently on the basis of the specificity of the organisms.

We attach the greatest significance to the data of ontogenetic development, considering that their application for the clarification of the interrelations of large groups of parasitic flatworms yields the most solid and convincing results.

We attach lesser importance to the data of comparative anatomy. However, we also use them to a considerable extent for large groups. We attach great importance to this body of data in examining smaller groups within a large group.

Finally, we use the specificity of the host and data on the host's phylogeny as supplements to the preceding criteria.

I. Ontogenesis and Phylogenetic Interrelations among Monogenea

The existing published data on the development of monogenetic trematodes are very inadequate. Particularly, this applies to information on postembryonic development and on the morphology of larvae of monogenetic trematodes. At the present time, the development of the representatives of only 10 genera is known, namely: Dactylogyrus (D. anchoratus Duj., D. crassus Kulw., D. vastator Nyb. -- works by Z. Kulwiec and others), Ancyrocephalus (A. vistulensis - A. siluri Zandt -- Siwak's works), Gyrodactylus (G. medius, G. elegans Nordm. -- works by Kathariner and others), Epibdella (E. melleni MacCallum -- work by Jahn and Kuhn), Dactylocotyle (D. luscae Ben. & Hesse -- work by Gallien), Polystomum (P. integerrimum Frol. -- works by Zeller, Halkin and others), Diplorchis (D. ranae Ozaki -- work by Ozaki), Sphyranura (S. oligorchis Alvey -- work by Alvey), Diplozoon (D. paradoxum Nordm. -- work by Zeller), and Udonella (U. caligi -- work by Beneden). Unfortunately, the data on Udonella are so inaccurate that it is impossible to take them into consideration.

In recent years (1928-1936), we have been able to restudy some of the genera that had been investigated earlier, as well as to investigate a number of new genera and families that have not yet been studied. The following genera and species were studied by us: 1) Dactylogyrus (D. vastator, D. wegeneri, D. crassus, D. anchoratus, D. cornu, D. fallax, D. crucifer) and a number of others; 2) Ancyrocephalus (A. siluri, A. bichowskii, A. cruciatus); 3) Gyrodactylus (about 15 species); 4) Polystomum (P. integerrimum); 5) Diplozoon (D. paradoxum); 6) Diplectanum (D. echeneis); 7) Calceostoma (C. inerme); 8) Nitzschia (N. elegans); 9) Octobothrium (O. alosae); 10) Microcotyle

(M. mugili); 11) Heteroonchus n. gen. (H. buschkieli n. sp.); 12) Tetraonchoides n. gen. (T. paradoxus n. sp.[1]).

Thus, we have at our disposal data on the development of 17 genera belonging to the following 10 families: DACTYLOGYRIDAE (Dactylogyrus, Ancyrocephalus, Diplectanum, Heteroonchus), CALCEOSTOMIDAE (Calceostoma), TETRAONCHIDAE (Tetraonchoides), TRISTOMIDAE (Epibdella, Nitzschia), UDONELLIDAE (Udonella), POLYSTOMIDAE (Polystomum, Diplorchis), SPHYRANURIDAE (Sphyranura), OCTOCOTYLIDAE (Octobothrium, Dactylocotyle, Diplozoon), MICROCOTYLIDAE (Microcotyle) and GYRODACTYLIDAE (Gyrodactylus).

The development of only 4 families remains completely unexplored (PROTOGYRODACTYLIDAE, MONOCOTYLIDAE, ONCHOCOTYLIDAE, and DICLIDOPHORIDAE).

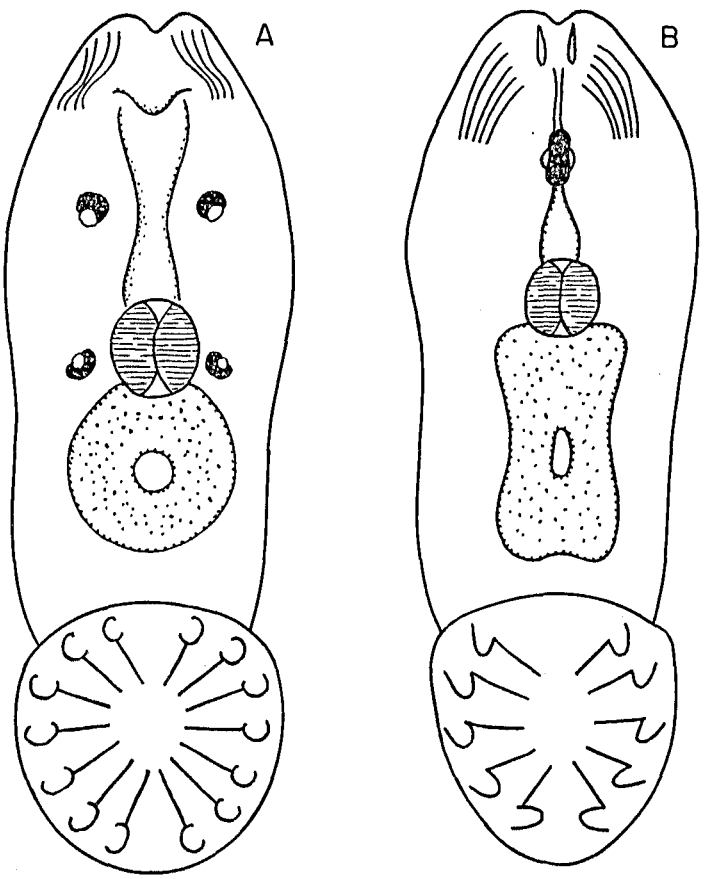

Figure 1. Larval types of Monogenoidea:
B - second larval type characteristic of Octocotylidae
A - first larval type characteristic of all other Monogenoidea.

Larvae of all studied forms may be classed in two basic types which differ greatly from one another and characterize, in our opinion, two main groups of monogenetic trematodes.

The first type of larvae (Figure 1), which is characteristic of all monogenetic trematodes studied with the exception of OCTOCOTYLIDAE and MICROCOTYLIDAE, is distinguished by the presence of a large number (14-16) of the so-called lateral hooks on the adhesive disc. These hooks on the larvae of this group are basically of one type: this is the so-called Dactylogyrus type of lateral hook (see Bychowsky, 1933b). This type of hook is distinguished by a hard, inflexible manubrium which

[1]For the description of both new species see Parasitological Collection of the Zoological Institute, USSR Academy of Sciences, No. 8.

develops gradually, and by a well-developed and curved point (Figure 2). Usually, larvae of this type have four well-developed eyes, although there may be no eyes at all in some forms (Tetraonchoides, Sphyranura).

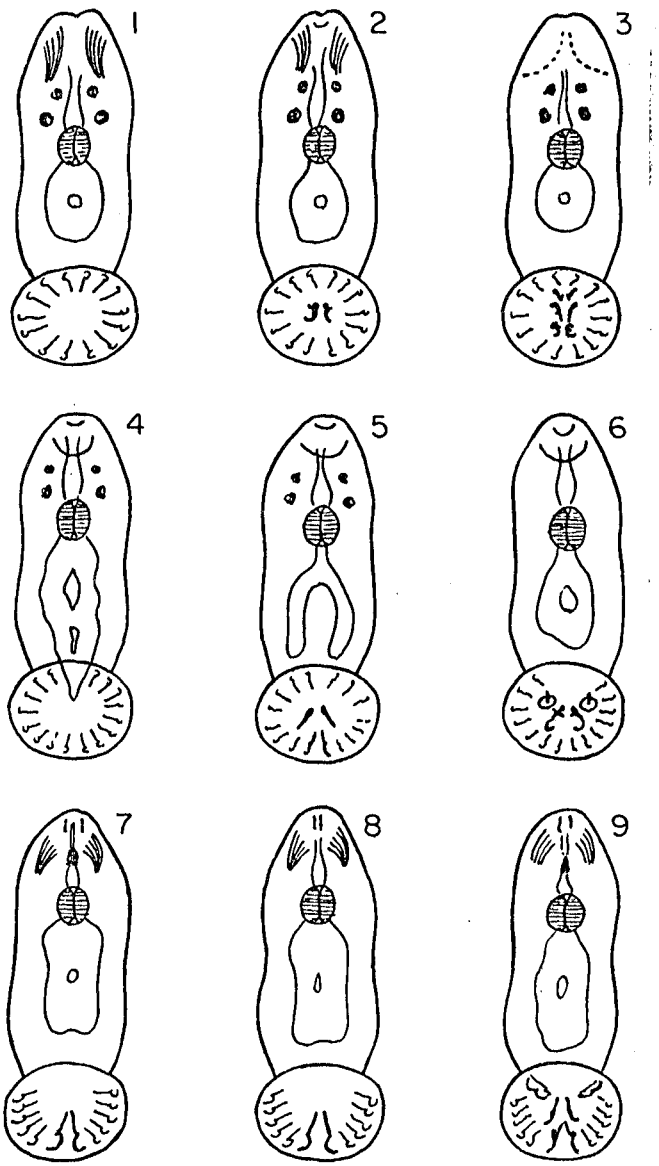

Figure 2. Changes in the adhesive disc of Monogenoidea larvae. The two upper rows belong to the first larval type, and the lower to the second type. 1 - Dactylogyrus larva, 2 - Calceostoma larva, 3 - Nitzschia larva, 4 - Polystomum larva, 5 - Diplorchis larva, 6 - Sphyranura larva, 7 - Octobothrium larva, 8 - Dactylocotyle larva

The second type of larvae characteristic of OCTOCOTYLIDAE and MICROCOTYLIDAE is distinguished by the presence of a comparatively small number of lateral hooks (10) on the attachment disc. These hooks differ in structure from those of the larvae of the first group. The manubrium of hooks of this type resembles a thin, very flexible elastic plate, and the point of the hook is more elongate and somewhat more weakly developed. Larvae of this type usually have one double eye or two separate eyes. Just as in the larvae of the first group, the eyes are sometimes completely absent (Dactylocotyle).

The presence of the lateral hooks, as well as their number, is extremely characteristic of not only the larvae of monogenetic trematodes, but also of their adult forms. It should be noted only that in the latter, due to the smallness of the lateral hooks, they are frequently not seen during examination (in some instances, it is impossible to discern all of the lateral hooks in adult forms). The regularity in the number of lateral hooks can be illustrated by a number of examples: in both genera of Protogyrodactylidae the number of lateral hooks is 12; in Dactylogyridae (20 genera),

16 genera have 14 lateral hooks each, one -- 12 (?), two -- 2 lateral hooks (?!), and one has none (??!). (Evidently, the data on the last four genera are not correct and are based on an insufficiently careful study.) In the only genus of MONOCOTYLIDAE which has been studied sufficiently in this respect, the number of lateral hooks is 14: in four of the genera of TRISTOMIDAE studied, the number of lateral hooks also is 14; in POLYSTOMIDAE and SPHYRANURIDAE, the number of lateral hooks in the majority of their genera and species is 16, and in 1 genus is 14; in GYRODACTYLIDAE (2 genera), the number of lateral hooks is 16.

Thus, for all the numerous trematodes belonging to the first group, we see that the numbers of lateral hooks vary insignificantly (from 12 to 16), and most frequently their number is 14. Along with the lateral hooks, we also observed the so-called medial hooks on a number of larvae. These hooks are characterized by an increase in their number in some forms. Increases in the number of hooks were observed by us both on the larvae of the first and second groups.

The following series of larvae of the first group may serve as an example of this situation. The larva of Dactylogyrus has no medial hooks at all; the larva of Calceostoma has one pair of medial hooks; finally, the larva of Nitzschia has three pairs of medial hooks.

In the adult forms we also observe the presence of medial hooks; in some instances these medial hooks begin to develop not during the time of the development of the egg, but considerably later. For example, the adult form of Dactylogyrus has two medial hooks, while its larva, as was mentioned above, has none at all; the adult worms of Ancyrocephalus have two pairs of medial hooks, and their larvae have only one pair, etc.

Thus, many forms seem to go through a stage of more "primitive" genera. For example, Ancyrocephalus goes through the stage of "Dactylogyrus," etc.

It should be mentioned further that the larvae of both types may have still greater complications in the structure of the accessories of the adhesive disc. For example, Sphyranura (larva of the first type) already has a pair of weakly developed suckers characteristic of adult animals in place of one pair of hooks. In the second type of larva, as for example, in Microcotyle, a larva which has already emerged from the egg has one pair of so-called valves which (in large numbers) is the characteristic adhesive organ of the adult animals.

The fate of both the lateral and medial hooks in the further development of larvae into adult animals can follow one of two patterns: either all these attachment structures increase greatly in size (lateral hooks to a lesser degree than the medial) and play the role of adhesive organs during the entire life of the animal, as for example, in DACTYLOGYRIDAE, or they gradually lose their attachment significance (sometimes not increasing at all in size, and sometimes increasing

both in size and number -- the latter refers to medial hooks) and become something like "vestigial" structures.

In the latter cases, i.e., when the chitinoid accessories of the disc of the larva loses its significance, various formations become the organs of adhesion.

In the larvae of the first type, the chitinoid apparatus may be replaced by:

1) an adhesive disc increasing in size and finally developing into a kind of a "sucker" [CALCEOSTOMIDAE, MONOCOTYLIDAE, TRISTOMIDAE, UDONELLIDAE (?)];

2) an adhesive disc increasing in size upon which form special new suckers which serve chiefly for adherence [POLYSTOMIDAE, SPHYRANURIDAE, ONCHCOTYLIDAE [sic] (?)];

3) a new adhesive disc not homologous to the disc of the Acanthocotyle larva.

The chitinoid apparatus of the larvae of the second type may be replaced by:

1) newly formed valves on a somewhat expanding disc which assume the function of attachment (OCTOCOTYLIDAE, MICROCOTYLIDAE);

2) evidently, suckers with valves can also form on an expanding disc (DICLIDOPHORIDAE). Because of the absence of the data on the development of DICLIDOPHORIDAE, we classify this group tentatively with the second type (on the basis of the structure of the adhesive equipment and the reproductive system).

Proceeding from the above, we can now give an evaluation of the phylogenetic significance of the various attachment organs.

Basic significance should be accorded the attachment structures of larvae (and adult PROTOCYRODACTYLIDAE [sic], DACTYLOCYRIDAE [sic], CALCEOSTOMIDAE, TETRAONCHIDAE, etc.) as structures which, undoubtedly, have a more ancient origin than the other adhesive organs.

All "secondary" attachment organs play a lesser role in revealing the phylogeny of the large groups of monogenetic trematodes, but are extremely important for explaining the phylogenesis within the limits of the latter.

Finally, data on anatomical structure (chiefly on the reproductive system) should be applied only after having considered the data on the structure of the attachment organs, since the latter doubtless are, as can be seen from the above, extremely constant "phylogenetic" characteristics.

On the basis of our evaluation of different characteristics, we can outline the following evolutionary routes among monogenetic trematodes.

1. Line DACTYLOGYRIDAE - CALCEOSTOMIDAE - MONOCOTYLIDAE - TRISTOMIDAE.

This line of evolution of the monogenetic trematodes is characterized by the presence of 14 lateral hooks of the attachment disc, an increase in the number of medial hooks from one pair to three pairs (maybe even more?) with subsequent replacement of hooks as attachment structures by the disc itself.

The family PROTOGYRODACTYLIDAE should be included with this line as a side branch. This family is very close to the primitive representatives of this line, but differs by some special features of the structure of the reproductive apparatus and the presence of 12 lateral hooks of the adhesive disc. The family TETRAONCHIDAE and the new, as yet undescribed, family TETRAONCHOIDIDAE closely related to it should be considered also as a side branch. It is characterized by the presence of 16 lateral hooks of the attachment disc, and in all probability, by a decrease in the number of medial hooks and, finally, subsequent replacement of the hooks as attachment structures by the adhesive disc itself. Moreover, a simple tubular intestine is a characteristic trait of the latter branch.

One of the features of this entire line is the presence of a copulatory organ having chitinoid armature in the form of a tube in more primitive forms (the overwhelming majority). In more highly organized forms of this line, this tube disappears gradually and the copulatory organ becomes unarmed.

Due to the lack of homology of the attachment disc of the adult and larval forms, the position of Acanthocotyle is not very clear. Finally, the family UDONELLIDAE, in all probability, is close to this group, but because it has not been sufficiently studied, we hesitate to establish its exact position in the system.

2. Line GYRODACTYLIDAE - SPHYRANURIDAE - POLYSTOMIDAE - ONCHOCOTYLIDAE.

This line is characterized by the presence of 16 (or 14, as an exception) lateral hooks of the attachment disc, by constancy and, in part, increase in the number of medial hooks (from 1 to 2 pairs) with subsequent appearance of suckers on the attachment disc as adhesive organs of the adult forms.

This very monolithic group is also characterized by the appearance of a canalis genito-intestinalis in more highly organized forms. All of its representatives are characterized by the presence of the armature on the copulatory organ in the form of small chitinoid hooks arranged

like a crown (their structure and number are, undoubtedly, of taxonomic significance). GYRODACTYLIDAE, which are the most primitive representatives of this group, are viviparous, which somewhat obscures the possibility of comparing them with other forms, although the closeness of GYRODACTYLIDAE to the other three families is beyond any doubt.

As has been pointed out earlier, we have no data on the development of ONCHOCOTYLIDAE and have placed them close to other representatives on the basis of comparative anatomy. We should point out that the genus Diclibothrium was classified with this family, in all probability, erroneously and it should be transferred to the family OCTOCOTYLIDAE. However, this question is not quite clear at the present time, and we are planning to treat it in a special work.

3. Line OCTOCOTYLIDAE - DICLIDOPHORIDAE (?) - MICROCOTYLIDAE.

This line is characterized by the presence in the larvae of 10 lateral hooks of the attachment disc, increase in the number of medial hooks and, finally, the replacement of the hooks (functionally) by attachment valves.

Also characteristic of this group is the structure of the copulatory organ (a crown of chitinoid hooks), female reproductive system and the presence of two preoral suckers. The position of DICLIDOPHORIDAE cannot be established sufficiently exactly for the reasons given above.

Proceeding from the evolutionary paths noted within the Monogenea, we are establishing its new taxonomic divisions. From our point of view, the system which we are suggesting is considerably more natural than the present generally accepted system, although some details require additional supplementation.

The system given below has been developed to the family and subfamily level and only those genera are given which are typical for one or another group[1] are mentioned.

The class Monogenoidea (Beneden) Bychowsky (syn. Polystomoidea Baer).

Diagnosis: Cercomeromorphae having, in the adult state, an attachment apparatus at the posterior end of the body. Digestive system is present. Direct development without change of host. Larvae have intestines. Parasites of cold-blooded vertebrates, exceptionally on parasitic crustaceans, cephalopods and aquatic mammals.

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[1] The diagnoses given below are extremely short and do not give a full characterization of the group, however, they are quite sufficient for diagnostic purposes.

Subclass I: Polyonchoinea n. subcl.

Diagnosis: Monogenoidea having larvae with 12-16 lateral hooks on the attachment disc; usually provided with four eyes. The attachment apparatus of the adult forms consists of chitinoid armature arranged on the attachment disc; the latter is capable of changing itself into a powerful sucker, or 2-6 special suckers may form on it. The mouth opening is situated between two groups of "cephalic" glands sometimes being equipped with one terminal sucker.

1st Order: Dactylogyridea n. ord.

Diagnosis: Polyonchoinea having larvae with 12-16 lateral hooks on the attachment disc. The attachment apparatus of the adult forms consists of chitinoid equipment situated on the attachment disc, in a number of forms, the latter changes into a powerful sucker. Copulatory organ unarmed or armed with a chitinoid tube. The anterior end is equipped with two groups of cephalic glands, often forming special glandular "cushions" serving for adhesion: sometimes the latter form sucker-like depressions. In the latter case, these "suckers" are never connected with the mouth opening.

1st Suborder: Dactylogyrinea n. subord.

Diagnosis: Dactylogyridea which, in the adult state, have an attachment apparatus in the form of chitinoid armature consisting of 12-14 (16 ?) lateral hooks, 1-2 pairs of medial hooks and a rather complex connective apparatus (between the medial hooks). The copulatory organ always has a chitinoid tube, one testis. Biramous intestine; no lateral branches and anastomoses; in most cases both branches of the intestine become joined at the posterior end.

1st Family: DACTYLOGYRIDAE Bychowsky.

Diagnosis (according to Bychowsky, 1933): small to average Monogenea. The attachment disc is equipped with a number (in most cases, 14) of lateral hooks and 2-4 medial hooks. Oviparous. The ovary is rounded, vaginal duct is either present or absent (?); yolk glands are well developed. The copulatory organ is equipped with a chitinoid tube and one to three parts of various shapes, either connected or not, with it or between themselves. Parasites of freshwater and marine fish.

1st Subfamily: Dactylogyrinae Bychowsky.

Diagnosis (according to Bychowsky, 1933): DACTYLOGYRIDAE with an attachment disc equipped with 2 medial hooks and 14 lateral hooks. There is a vaginal duct, armed or unarmed. The ovary and testis are rounded. The intestinal crura fuse posteriorly. Parasites of freshwater fish and, exceptionally, of marine fish. Type genus: Dactylogyrus Diesing.

2nd Subfamily: Ancyrocephalinae n. subfam.

Diagnosis: DACTYLOGYRIDAE with an attachment disc equipped with 4 medial hooks and 14 lateral hooks (as an exception, there may be 16 -- it needs verification !). The vaginal duct is either present or absent. The ovary and testis are mostly rounded or retort-shaped. The crura may fuse at the posterior end or terminate as a cul-de-sac. Parasites of marine and freshwater fish. Type genus: Ancyrocephalus Creplin.

3rd Subfamily: Diplectaninae (Monticelli) Bychowsky (syn. Lapidotreminae J. & T.).

Diagnosis: DACTYLOGYRIDAE with an attachment disc mostly with 14 lateral hooks and four medial hooks, and two special plate-like organs ("Squamodisc") with scale-like papillae arranged in rows. Moreover, in the majority of the genera a considerable part of the body is covered by scale-like papillae. In many genera, the squamodisc has additional hooks. Two pairs of eyes. The crura do not fuse at the posterior end of the body. The copulatory organ is either simple or complex, and is chitinoid. A vaginal duct is present. Parasites of marine and fresh water fish. Type genus: Diplectanum Diesing.

It is interesting to note the fate of the type genus of this subfamily. In 1903, Maclaren classified the representatives of this genus with the genus Tetraonchus (Ancyrocephalus e.p.) as a separate subgenus. Later, in 1909, Lühe made the genus Tetraonchus a syn. of the genus Ancyrocephalus Creplin, and Diplectanum began to be automatically classified with the latter genus. Then, even a separate subgenus (Johnston & Tiegs) was elimated in the revision of Gyrodactyloidea published in 1922. At the same time these two authors described a new subfamily Lepidotreminae which differed mainly by the presence of a squamodisc. However, in reality, it appears that the genus Diplectanum has nothing in common with Ancyrocephalus and that it is characterized by the same features upon which Johnston & Tiegs based their subfamily Lepidotreminae. These authors included Diplectanum in the genus Ancyrocephalus simply because they were unfamilar with the appropriate literature. Thus, it should be considered that Monticelli was absolutely correct when in 1903 he isolated Diplectanum as a separate subfamily Diplectaninae whose syn. is, consequently, Lepidotreminae Johnston & Tiegs.

2nd Family: PROTOGYRODACTYLIDAE Johnston & Tiegs.

Diagnosis (after Johnson & Tiegs, 1922): small Dactylogyrinea. The width and the length of the body are almost equal. A well-developed attachment disc has two pairs of comparatively large medial hooks and numerous small ones (12). The cephalic glands open at the anterior end into prostomia. The intestine is bifurcated; its crura fuse at the posterior end and terminate blindly. There is no vaginal duct.

The uterus is very short. The cirrus is a simple chitinoid tube included in a cirrus sac. The vitelline system is extremely remarkable: it consists of numerous yolk "tubes" which are divided on each side of the body into anterior and posterior groups (in relation to the ovary). Transverse yolk ducts become united into a long medial duct opening into the ootype. The rear transverse duct of the yolk glands is clearly connected with the alimentary canal. Parasites of fresh water fish. Type genus: Protogyrodactylus Johnston & Tiegs.

2nd Suborder: Tetraonchinea n. subord.

Diagnosis: Dactylogyridea, in the adult state having an attachment apparatus in the form of chitinoid armature consisting of 16 lateral hooks and 1-2 pairs of medial hooks, and a connective apparatus. The attachment disc can become sucker-like. The copulatory organ always has a chitinoid tube; there is one testis. The intestine is in the form of one crus.

1st Family: TETRAONCHIDAE (Monticelli) Bychowsky.

Diagnosis: Tetraonchinea, in the adult state they have an attachment apparatus in the form of chitinoid armature consisting of 16 lateral hooks, 2 pairs of medial hooks and one connective plate. Parasites of fresh water and migratory fish. Type genus: Tetraonchus Diesing.

The new family TETRAONCHOIDIDAE (see page 4) also belongs to this suborder.

3rd Suborder: Monopisthocotylinea Odhner.

Diagnosis (after Fuhrmann, 1928): monogenetic trematodes with a flattened or rounded body. The anterior end with or without lateral suction depressions. The posterior end has a large adhesive disc in the form of a sucker, often subdivided by septa, most frequently with chitinoid hooks. Eyes are often present. The pharynx is well developed. The intestine is bifurcated, most frequently with lateral branches. The male porus genitalis and the opening of the uterus are situated medially or laterally. There are 1-2 or more testes. The vaginal duct is single or double, less frequently it is absent (?). Canalis genito-intestinalis is always absent. Live on the skin or gills of marine fish (as an exception, on migratory or even fresh water fish).

1st Family: CALCEOSTOMIDAE (Parona & Perugia) Mongicelli.

Diagnosis (Partly after Johnston & Tiegs, 1922): Monopisthocotylinea in which cephalic glands open in a more or less scattered way on both sides of the anterior end. The adhesive disc shows a tendency toward forming a sucker, however, the latter is less developed than in the subsequent families. In connection with this,

the medial hooks are reduced and even disappear (?). Eyes are either present or absent. The intestine is with or without lateral branches. There is only one testis. The ovary is either simple or branched. The cirrus is simple. A vagina is either present or absent. Parasites of salt water fish. Type genus: Calceostoma Beneden.

2nd Family: MONOCOTYLIDAE Taschenberg.

Diagnosis (after Johnston & Tiegs, 1922): small Monopisthocotylinea lacking cephalic glandular organs, in place of which numerous glands open. The adhesive disc is transformed into a sucker. Eyes are either present or absent. The testis is simple and compact or split up into follicles. The ovary is simple. A vaginal duct is present, and is usually paired. The intestine is biramous, most frequently simple, and less frequently with side branches. Parasitic on gills of Elasmobranchia. Type genus: Monocotyle Taschenberg.

This family is usually divided into two subfamilies, Monocotylinae and Pseudocotylinae, and some authors even isolate a third subfamily: Calicocotylinae. Because of the absence of data on the development of the family, its subdivision into subfamilies does not appear sufficiently clear to us, although the division into two subfamilies is more or less natural. The genus Acanthocotyle occupies a special position within the family for the reasons which have already been pointed out several times before.

3rd Family: TRISTOMIDAE Monticelli.

Diagnosis: average or large Monopisthocotylinea with well developed cephalic glandular organs which often have a sucker-like shape. The adhesive disc has the form of a large powerful sucker. Eyes are present in the majority of cases. The testis is single, double, or consists of numerous follicles. The ovary is usually simple. The vaginal duct is either present or absent. The intestine is biramous, most frequently with lateral branches. Parasites of salt water fish. Type genus: Tristoma Cuvier.

The family is divided into two subfamilies: Ancyrocotylinae characterized by the absence of septa on the adhesive disc and Tristominae in which the posterior sucker is divided into parts by septa. In all probability, the subdivision is natural, but since we have no data on the development of Tristominae, we do not consider it possible to make a final decision regarding the subdivision.

Supplementary: the family UDONELLIDAE Beneden & Hesse.

For the reasons mentioned above, the position of this family in the system of Monogenoidea is not clear. In all probability, this family is an extremely degraded group of Monopisthocotylinea.

2nd Order: Gyrodactylidea n. ord.

Diagnosis: Polyonchoinea having larvae with 16, less frequently 14 (?) lateral hooks on the attachment disc. The attachment apparatus of the adult forms consists of chitinoid armature situated on the attachment disc; more highly organized groups have 2-6 suckers on the adhesive discs. The copulatory organ has a crown of chitinoid hooks or is unarmed (?). The anterior end has two groups of cephalic glands. The mouth opening often has a terminal sucker. Forms which do not have suckers on the disc are viviparous, the others are oviparous.

1st Suborder: Gyrodactylinea n. subord.

Diagnosis: Gyrodactylidea which in the adult state have an attachment apparatus in the form of 16 chitinoid lateral hooks and one pair of medial hooks, or without the latter. Those which have medial hooks also have a connective apparatus. The intestine is biramous with branches which do not merge at the posterior end. Viviparous.

1st Family: GYRODACTYLIDAE Beneden & Hesse.

Diagnosis: small elongated Gyrodactylinea with a well-developed attachment disc equipped with 16 lateral hooks and one pair of medial hooks. The latter may be absent. The ovary is V-shaped; there is no vaginal duct and yolk glands. Parasites of fresh water and marine fish and cephalopods. Type genus: Gyrodactylus Nordmann.

The isolation of Isancistrum as a separate subfamily is artificial because the absence of medial hooks within this group is not a characteristic of great significance, as it is, for example, in the case of Dactylogyridea.

2nd Suborder: Polyopisthocotylinea (Odhner) Bychowsky.

Diagnosis (partly after Fuhrmann, 1928): Gyrodactylidea with a more or less elongate body, flattened at the posterior end, and having an attachment disc with chitinoid hooks and 2-6 suckers. In addition, some have a small outgrowth of the disc which is equipped with two small suckers. The mouth opening has a single simple sucker or a sucker-like expansion. The intestine is biramous, often with anastomoses and lateral branches; the crura often fuse posteriorly. The male copulatory organ has a crown of chitinoid hooks. There is often a vaginal duct, which is usually double. Canalis genito-intestinalis is present. Oviparous.

1st Family: POLYSTOMIDAE Carus.

Diagnosis: flattened Polyopisthocotylinea with a more or less well-developed oral sucker. The attachment disc has 6 suckers and

chitinoid hooks (14[1]-16 lateral; 1-2 pairs medial). The male porus genitalis and the uterine pore are medial. The vaginal ducts are double, opening on the sides of the body; as an exception, they may be absent. Parasites of amphibians and reptiles, and, as an unverified exception, of aquatic mammals (hippopotamuses). Type genus: Polystomum Zeder.

2nd Family: SPHYRANURIDAE Poche.

Diagnosis: flattened Polyopisthocotylinea with a well-developed oral sucker. The attachment disc has 2 suckers, 16 lateral hooks, and 1 pair of medial hooks. The male porus genitalis and the uterine pore are medial. There are either no vaginal ducts, or they terminate blindly. Parasites of amphibians. Type and only genus: Sphyranura Wright & MacCallum.

3rd Family: ONCHOCOTYLIDAE Cerfontaine.

Diagnosis (after Fuhrmann, 1928): lanceolate Polyopisthocotylinea with a widened attachment disc which continues to form a small outgrowth. The disc has 6 large suckers on it each of which has a large hook bent like a sickle. The appendage of the disc has 2 small suckers with 2 small hooks between them (medial hooks ?). The mouth opening is in a terminal position and has a large sucker. The porus genitalis is medial. The vaginal duct is double. The intestine is biramous; at its posterior end the branches fuse and enter the attachment disc. Parasites of Selachia. Type genus: Onchocotyle Diesing.

We have placed this family with Polyopisthocotylinea on the basis of comparative anatomy because, as we have already pointed out, we have no data at all on its development.

Subclass II. Oligonchoinea n. subcl.

Diagnosis: Monogenoidea having larvae with 10 lateral hooks on the adhesive disc, mostly provided with two eyes or one double eye. The attachment apparatus of the adult forms consists of chitinoid valves arranged on the adhesive disc, sometimes within suckers. The mouth opening has two suckers closely associated with it.

1st Order: Octocotylidea n. ord.

Diagnosis: Oligonchoinea with the characteristics of the subclass.

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[1]The data regarding 14 lateral hooks are doubtful; these data are a result of the fact that one pair of lateral hooks is sometimes of a larger size than the other 14.

1st Family: OCTOCOTYLIDAE Beneden & Hesse.

Diagnosis (after Fuhrmann, 1928): heterogeneous family of ectoparasitic trematodes with an elongate body having an attachment disc with 4, 5, 6, or in most instances 8 valves, and with hooks. The oral infundibulum has 2 suckers. The intestine is double, branching, or, less frequently, tubular and also branching. Genital hooks are present. A vaginal duct is present, single or double, or it is absent. Parasites of marine and fresh water fish. Type genus: Octocotyle Diesing.

As mentioned in the diagnosis, in all probability this family is heterogeneous and requires further research.

Let us mention that it seems to us that the genus Protomicrocotyle Johnston & Tiegs should be placed within Octocotylidae, but only after additional study, because MacCallum's material, in all probability, was kept unfixed too long before study, and therefore, was inadequate not only for describing the genus but even for species description. In any case, isolation of this genus into a separate family, as was done by Poche, is absolutely inadmissible. At the same time let us note that the families PLACTANOCOTYLIDAE [sic] Poche, PLATYCOTYLIDAE Monticelli, and GRUBEIDAE Poche which are recognized as distinct families, we include at present in with the family OCTOCOTYLIDAE due to the absence of data on ontogenesis within these groups.

2nd Family: MICROCOTYLIDAE Taschenberg.

Diagnosis (after Fuhrmann, 1928): ectoparasitic trematodes with a greatly widened posterior end (attachment disc) with numerous symmetrically or asymmetrically arranged small valves. The mouth opening has two suckers. The genital atrium is medial and equipped with chitinoid hooks. A vaginal duct is present. Parasites of marine fish. Type genus: Microcotyle Beneden & Hesse.

3rd Family: DICLIDOPHORIDAE Cerfontaine.

Diagnosis (after Fuhrmann, 1928): monogenetic trematodes with an attachment disc equipped with 8 large suckers, or 6 large and two rudimentary ones within which complex chitinous trabeculae (valves) are arranged. The mouth opening has 2 lateral suckers. The intestine is bifurcated and branching. The penis has a crown of chitinoid hooks. No vaginal duct. Parasites of marine fish. Type genus: Diclidophora Gota, [sic].

The taxonomic position of the latter family is not quite clear. On the basis of the structure of the oral opening which has two lateral suckers, the structure of the chitinoid trabeculae of the suckers and other characteristics, we place DICLIDOPHORIDAE with the order Octocotylidea, although it is possible that after studying further

representatives of this family, it will be necessary to separate it as an independent order. However, the position of Diclidophoridea in the subclass Oligonchoinea seems to us certain in spite of the absence of ontogenetic data.

In concluding the first part of our report, it is necessary to stress once again that some parts of the system suggested by us require further study and verification. However, we believe that the main evolutionary paths of this group have been fully explained and should not be greatly modified due to some new data on development and comparative anatomy of Monogenoidea.

II. Brief Historical Survey of Opinions Regarding the Origin of Individual Groups of Parasitic Flatworms

In order to clarify the position of Monogenea in the Platoda system, it is necessary to dwell briefly upon the problem of the origin of the entire group of parasitic flatworms.

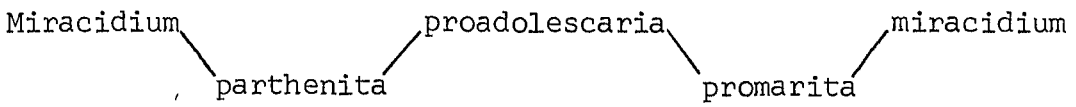
According to a generally accepted view, parasitic flatworms are derived from Turbellaria. This is based, chiefly, on a comparison of the structure of sexually mature, hermaphroditic parasitic flatworms with adult Turbellaria. However, there is also a different viewpoint which was advanced by D.F. Sinitsin. This author writes in his work on the parthenogenetic generation of trematodes in Black Sea molluscs: "Placing digenetic trematodes in the class Platodes is, of course, based on a misunderstanding . . . There is no doubt that trematodes originated from more highly organized invertebrates, but from what? It is impossible to answer this question definitely, because we do not have sufficient data for this, but it is still possible to reach at least an approximate conclusion on the basis of a scheme which we have developed for a hypothetical proparthenita. On the one hand, it resembles Trochelmintae, and, on the other hand, - Arthropoda: all these forms are characterized by the absence of a ciliated covering, instead of which they have a developed cuticulum and external skeleton, a peculiar body cavity, a peculiar metamerism, and a permanent posterior end of the body. Finally, if we add to this the ability for parthenogenetic reproduction and heterogeny common to these forms does not appear so unusual."

Thus, according to D.F. Sinitsin, some of the parasitic flat worms are not connected genetically with Turbellaria and, consequently, the entire group is artificial and united on the basis of a convergent similarity in the structure of maritae, i.e. sexually mature hermaphroditic individuals. Let us also note that, according to the same author, Monogenea, at least a part of them, originated from Digenea through simplification of the life cycle of the latter.

According to Sinitsin, the primary form of trematodes (a protrematode) was a form with heterogeny leading a free-living existence. The life cycle of these forms is represented by the author in the following scheme:

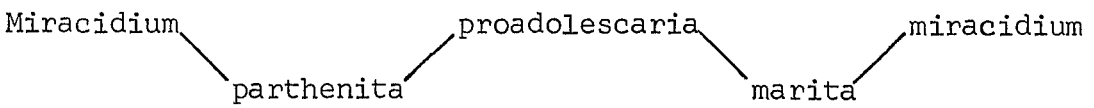
Miracidium-proparthenita-proadolescaria-promarita-miracidium.

Further, the parathenogenetic generation changed to parasitism in molluscs. Accordingly, the scheme of the cycle changes to:



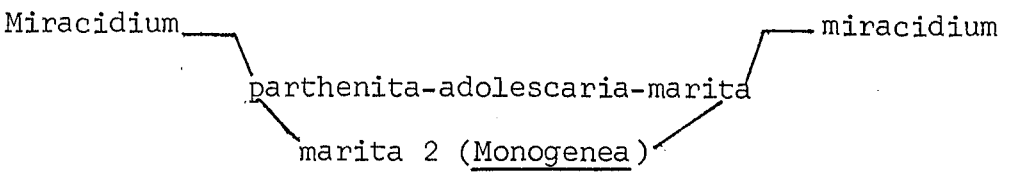
(Mollusca - I host)

Finally, the third period is that of the adaptation of the maritae to parasitism:



(Mollusca - I host) (Vertebrata - II hosts)

Further progress of the evolution of Digenea is clear, but Sinitsin derives Monogenea from the last scheme through simplification of the life cycle. This proposal is clear from the following scheme:



In connection with the above theory, it is necessary to clarify the origin of the phenomenon of intermediate hosts in the case of heterogeny in order to solve the problem later on of the possibility of comparing the various stages of development. Our view of this problem coincides to a considerable degree with the opinion of Looss (1892) and Mordvilko (1908), who believe that the primary host is the final host (vertebrate), and the secondary host is the intermediate (mollusc). In any case, we consider the marita, according to Sinitsin's terminology, to be the primary parasitic form. This decision will also be important for us later, and at present it solves the problem only from Sinitsin's point of view. It should be rejected on the basis of the fact that his primary trematode is derived by him from the redia which, in our opinion, is not primary, because rediae are more modified development stages of Digenea than is the marita. As for the origin of Monogenea from Digenea, we shall return to it later.

Thus, we agree with the generally accepted view of the origin of parasitic flat worms from Turbellaria.

Now it is necessary to consider from what groups of Turbellaria various groups of parasitic flat worms are derived. Answers to this question vary. The majority of authors are inclined to derive parasitic flat worms from Rhabdocoela, and only a few, as, for example, Lönnberg and Wilchelmi, derive Monogenea and Digenea from Triclada. We shall not elaborate upon the last viewpoint, because it has been rejected almost completely. There are too many objections against it. The most important of them is the constant presence of two ovaries in Triclada, while there is only one in Trematoda; differences in the structure of the female genital system, etc.

There is no doubt that the conclusion that parasitic flat worms originated from Rhabdocoela is more consistent with data of comparative anatomy, and it should be recognized as correct.

However, the above refers to the origin of the entire group as a whole. As for individual groups of parasitic flat worms, the viewpoints of various authors in this respect are diametrically opposed.

According to Janicki, all groups of parasitic flat worms originate phylogenetically from one another. Therefore, there is one common stem: Rhabdocoela-Monogenea-Digenea-Cestoda.

According to Meixner, Fuhrmann and others, Cestoda originated directly from Rhabdocoela. Trematoda originated from the latter as an independent branch and, in all probability, Monogenea originated from Digenea.

As it has already been mentioned, Sinitsin derives at least a part of Monogenea from Digenea.

Finally, Sqendel derived Cestoda from Monogenea.

Janicki's opinion is based on his "cercomera" theory. According to this theory, the attachment disc of Monogenea is a prototype of the "cercomere," i.e., the tail outgrowth of the larvae of Digenea and Cestoda. The presence of the cercomere in all three groups compelled Janicki to combine them in a special class of Cercomorpha which was juxtaposed by him against Turbellaria. There are many objections to this theory, particularly against Janicki's suggestion regarding the origin of Cestoda from Digenea. The main objection raised by Fuhrmann is that the high specialized organization of Digenea and Cestoda makes it impossible to derive the latter from the former, and also the different types of development (Digenea larvae in molluscs, Cestoda larvae in crustaceans), etc.

The second viewpoint regarding the independent origin of Cestoda and Digenea-Monogenea is based on similarities in the anatomy of Digenea-Monogenea, on the one hand, and Cestoda, on the other, directly to Rhabdocoela (chiefly, ANOPLODIIDAE).

The third viewpoint (Sqendel), which coincides with our opinion, does not require any special discussion, just as Sinitsin's did not. Our attitude toward this viewpoint will be obvious from further explanations.

We do not consider it necessary to dwell in detail upon this subject, because it would require a considerable amount of time and would cause us to digress in the direction of special bibliographical studies which do not have any fundamental significance for the views discussed below.

III. Interrelationship of Monogenea and Cestoda with Digenea

In order to attempt to schematize phylogenetic interrelations of parasitic flatworms (Figures 3 and 4), it is necessary, first of all, to understand the interrelations between Monogenea and Digenea, on the one hand, and Digenea and Cestoda, on the other.

As can be seen from the first part of this report, we are attaching extremely great phylogenetic significance to the attachment disc of Monogenea, whose development, in our opinion, is a very ancient occurrence which characterizes the entire group as a whole. In this respect, our opinion is close to that of Janicki, who, as has been pointed out earlier, considers this formation very important phylogenetically.

Comparing Digenea with Monogenea we see that the former do not have a structure homologous to the attachment disc of Monogenea.

This fact is extremely important for our entire concept and, therefore, we shall examine it in more detail. First of all, it is necessary to raise the question of what developmental stage of Digenea can be compared with a larva of Monogenea which has just emerged from an egg? If we consider that the primary form of Digenea (see above) is a hermaphroditic worm, then, consequently, its larva, i.e., miracidium, is equivalent to a larva of sexually mature Monogenea. The comparison of a miracidium and a Monogenea larva reveals their completely different structure. Monogenea larvae are characterized by the presence of an attachment disc with chitinoid armature, the presence of a rather well developed digestive system, etc. The miracidium is characterized by the absence of the attachment disc or any outgrowth of the posterior end, particularly of its armature, by the absence of an intestine, etc. However, it should be mentioned that Aspidogaster conchicola produce eggs from which larvae with intestines emerge; however, from our point

of view, the larva of Aspidogaster conchicola is not homologous to the miracidium of other Digenea. The presence of traces of an intestine in some forms (Schisostoma, Diplodiscus) seem to require detailed verification.

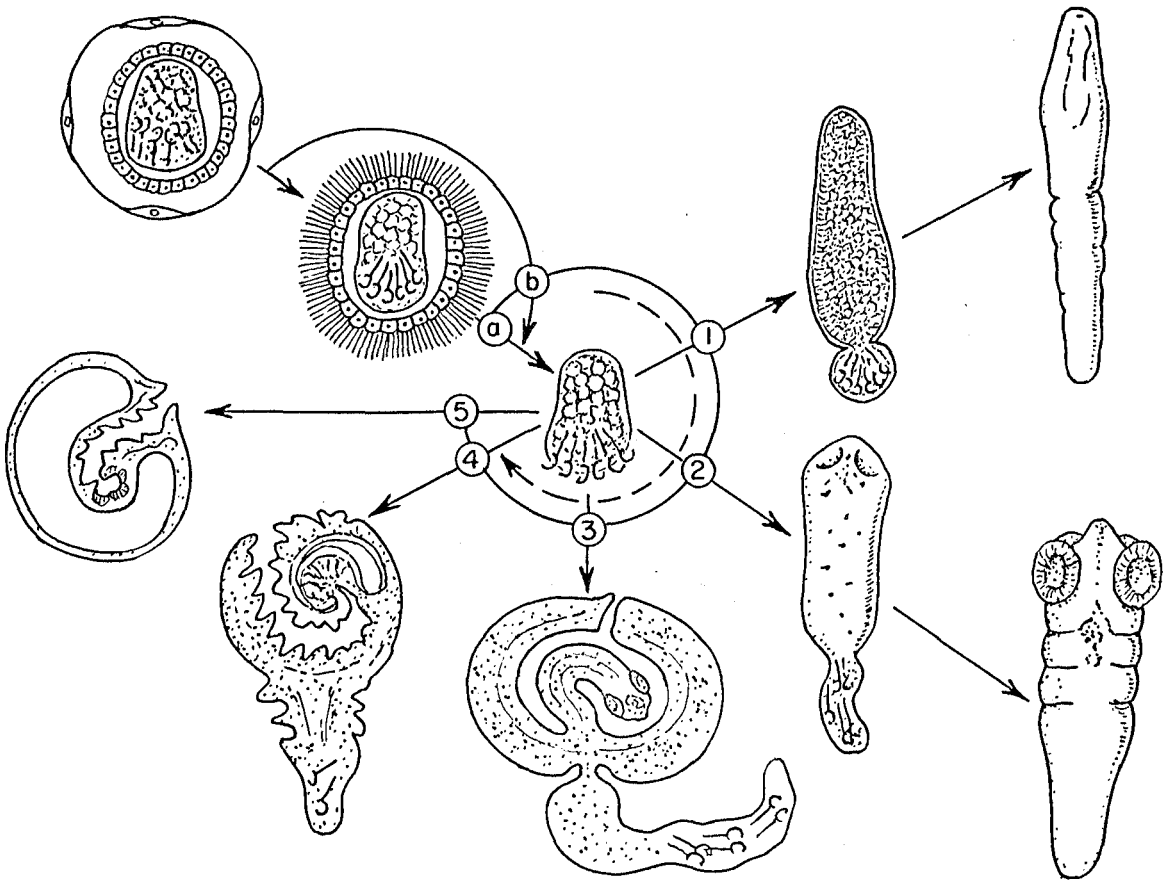


Figure 3. Diagrammatic scheme of development of Cestoidea. a - development with a coracidium, b - development without a coracidium, 1 - Pseudophyllidea, 2 - Tetraphyllidea (Proteocephalidae), 3-5 - Cyclophyllidea.

Even if we disregard the fundamental aspect of the problem and attempt to compare the attachment disc of the Monogenea larva with the tail of the cercaria, i.e. with the structure of a phylogenetically younger larva, we shall see the nonequivalence of these two structures (cf. Janicki's theory!). The tail of a cercaria develops in an entirely different manner than the disc of Monogenea. The former forms anew at the posterior end of the body, while the latter is an isolated

part of the posterior end of the body (see works on the development of Digenea by Sinitsin and others). The attachment disc of Monogenea always has chitinoid armature (with the exception of Udonellidae - requires verification!), while the tail of a cercaria is never equipped with them. The difference between these two structures is emphasized even more by the structure of the excretory system.

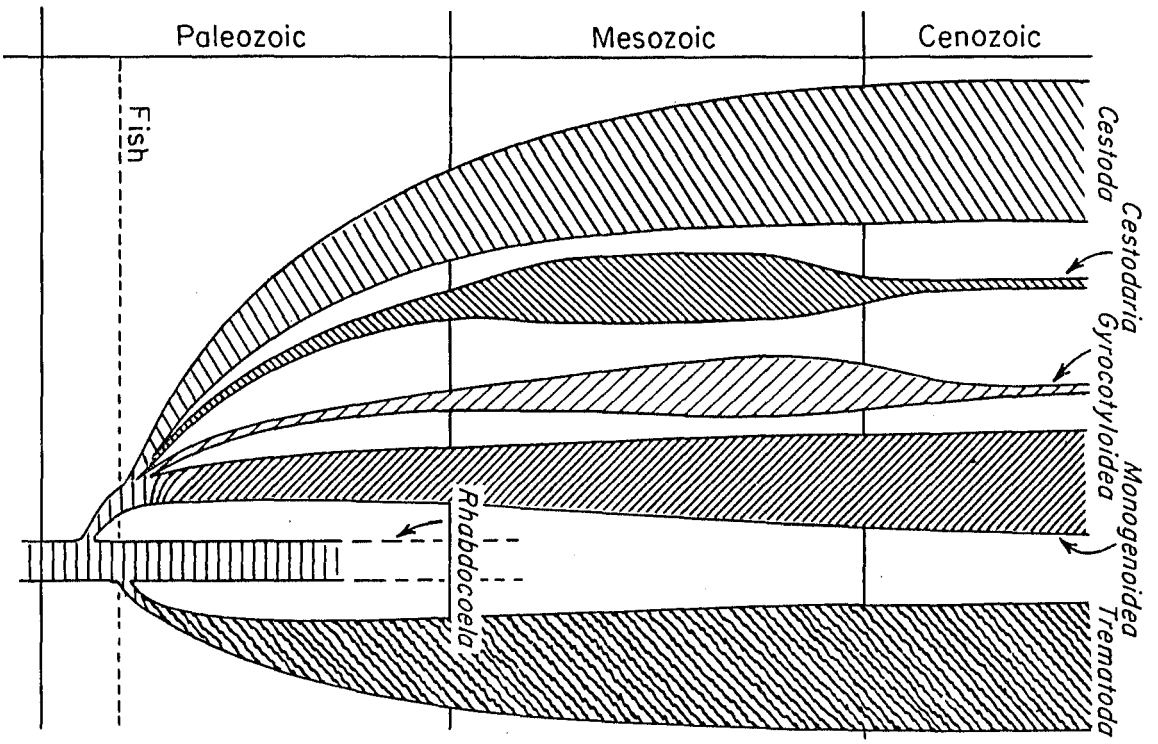


Figure 4: Evolutionary scheme of parasitic flatworms.
Key: 1) Paleozoic 3) Cenozoic
2) Mesozoic 4) Fish

The above facts alone are sufficient to make us be cautious with regard to identifying Digenea closely with Monogenea. Without dwelling on the details of similarities in the structure of adult Monogenea and hermaphroditic sexually mature Digenea due to lack of space, we consider that these resemblances are purely convergent and do not indicate at all that these two groups are phylogenically related.

A most detailed and thorough comparison of Monogenea and Digenea compels us to accept as an indisputable fact that these two groups have independent origins, although, as can be seen from the above, they originated from more or less closely related ancestors. The presence in Monogenea of a "cercomere," i.e. an attachment disc with chitinoid armature, and its absence in Digenea should be considered as characteristic. The modern Digenea are also characterized by the presence of alternation of generations, unlike Monogenea, which have primary direct development. The absence of alternation of generations in Aspidogaster conchicola (which has not yet been proved definitely!) is, undoubtedly, a secondary phenomenon.

As for the relationships between Digenea and Cestoda, it should be mentioned here that the generally accepted idea regarding the origin of Cestoda from Digenea is completely erroneous. We quite agree with Fuhrmann, who writes: "It is unlikely that the highly-specialized digenetic Digenea living in the intestine would produce the no less highly specialized monogenetic Cestoda also living in the intestines of vertebrates. Probably, the primary forms of both groups are of different origins and have different routes of development. The external morphology of Digenea and, particularly, the arrangement of the attachment organs are completely different from those of Cestoda, and this difference could not have disappeared in Cestoda in the host's intestine. It should be mentioned that the similarity in the structure of the reproductive apparatus is not at all significant and exists only to a certain degree in Bothriocephalida which are not at all primitive. The uterus does not open next to the cirrus-pouch into the genital atrium in any Cestoda. If, as is accepted, Laurer's canal is homologous with the vaginal duct, then the difference between classes becomes still greater. The development of both groups is completely different; moreover, Digenea's primary larvae which multiply parthenogenetically always have Mollusca as a host, while primary larvae of Cestoda (procercoid) are always in the body cavity of Crustacea.

Thus, as has been mentioned earlier, we believe Digenea are quite distant from Monogenea and Cestoda, and, undoubtedly, the first group has a different origin from the other two. This is confirmed even more by the further analysis of the interrelationship of Monogenea and Cestoda.

Before we begin a discussion of the latter question, we should mention that the attempts which have already been made to divide the Trematoda into two independent classes corresponding to Monogenea and Digenea are absolutely correct and indicate the different origins of these two groups. As one can see from the first part of our report, we also segregate Monogenea as a separate class, Monogenoidea, in the system we suggested.

IV. The Position of GYROCOTYLIDAE in the System of Flatworms

Before we discuss the interrelationship of Monogenea and Cestoda, it is necessary to discuss the position of the family GYROCOTYLIDAE in the system of parasitic flatworms. This distinctive group, consisting at present of only two genera, belongs, according to the current taxonomy, to the subclass Cestodaria as a separate order, Gyrocotylidea, which has no connection with the second order, Amphilinoidea, with respect to its morphology and anatomy.

First of all, it should be mentioned that even the problem of body orientation of these animals was not made clear until very recently. In his last summary, Fuhrmann (1931) (just as did Spencer, Lönnberg and Dollfus earlier) assumes that the anterior end is the one which has a rosette. He considers that this is proved, firstly, by the movement of the animal with the rosette forward and, secondly, by the fact that the spines situated in the cuticle are directed backward with this orientation, i.e., as all Trematoda and Cestoda which are provided similarly. Fuhrmann writes: "If the orientation would be opposite, the spines would be directed forward, which never occurs in the animal kingdom." A contrary view was held by Wagener, Monticelli, Braun, Ward, Kofoid, Watson, and Woodland who believed that Gyrocotyle's rosette was homologous to the attachment disc of Monogenea, thus considering it to be at the posterior end of the animal. In spite of the fact that this point of view may seem unlikely at first glance (taking into consideration Fuhrmann's reasonings), it was brilliantly confirmed by Ruszkowski's work on the larvae of Gyrocotyle urna published in 1932. During his studies, the author was able to detect four rather large larvae which had embryonic hooks at the end with a rosette. These facts are an indisputable proof of the correctness of regarding the rosette as being a formation at the posterior end of the body, which, thus, solves the question of the body orientation of GYROCOTYLIDAE.

Taking into consideration the solution of the problem of body orientation of GYROCOTYLIDAE, we analyzed the anatomy of these worms, comparing it with that of Monogenea and Cestoda, with completely unexpected results.

The presence of the attachment structure at the posterior end of the body is a feature characteristic only of Monogenea (except for GYROCOTYLIDAE). The presence of the armature of the cuticle in the form of distinctive spines equipped with special muscles, which never occur in Cestoda because their hooks have an entirely different structure, brings GYROCOTYLIDAE closer to Monogenea, some of which (for example, Diplectaninae) have such formations.

The structure of the cuticle of GYROCOTYLIDAE is the same as that of Cestoda and Monogenea.

Muscles with a well developed layer of diagonal fibers, which occurs rarely in Cestoda (for example, in some species of the Hymenolepis), are characteristic of Monogenea.

GYROCOTYLIDAE are characterized by the absence of calcareous bodies in the parenchyma, while this is not usual in Cestoda.

The excretory system of GYROCOTYLIDAE is quite distinctive. It is represented by a greatly branching system of vessels among which it is impossible to distinguish the main trunks. Within the vessels, almost in all large trunks, there is a peculiar "ciliary fringe." Such structures never occur in Cestoda. It is particularly interesting that the excretory system of GYROCOTYLIDAE has two apertures arranged laterally in the area of the genital pores. This never occurs in Cestoda, but is a most characteristic feature of Monogenea.

The nervous system is organized in the same way as in Monogenea with a well developed attachment disc. Both these Monogenea and GYROCOTYLIDAE are characterized by the presence of a powerful nerve ring in the posterior organ, of attachment.

Gyrocotyle fimbriata has two sensory papillae arranged near the acetabulum at the anterior end of the body, and a little farther, laterally and ventrally, two elongated and recessed papillae with a special cuticular lining and rich innervation. These structures are treated as sense organs (of an unknown function). Cestoda do not have such structures, but Monogenea (Polyonchoinea) are characterized by the presence of two head organs which, undoubtedly, also have a sensory function, and, beyond any doubt, are homologous to the above-mentioned structures in Gyrocotyle fimbriata. (Undoubtedly, Gyrocotyle urna also has the cephalic organs.)

GYROCOTYLIDAE have no digestive system at all, which absence is a characteristic of Cestoda and not of Monogenea.

The male genital system of GYROCOTYLIDAE is characterized by a large number of testes situated toward the front of the ovary. This arrangement is common in Cestoda, but very rare in Monogenea. The male genital pore of GYROCOTYLIDAE has a special opening and is situated near the opening of the uterus. The copulatory organ has the form of a retractile penis, which is characteristic of many Monogenea and does not occur in Cestoda, in which a cirrus with rather pronounced bursa cirri is common.

The ovary in GYROCOTYLIDAE is bilobate, of an extremely unusual follicular structure resembling that of some Polyclada. In general, the presence of a bilobate ovary is characteristic of Cestoda and occurs in Monogenea only as an exception (GYRODACTYLIDAE). However, the structure of the ovary in GYROCOTYLIDAE is, probably, also quite different from the cestoid type.

The vaginal duct of GYROCOTYLIDAE opens near the edge of the body, in the vicinity of the male genital pore and opening of the uterus, but is dorsal and not ventral as these two openings are. Such an unusual arrangement of the vaginal duct openings never occurs in Cestoda, but quite frequently in Monogenea, as, for example, in MICROCOTYLIDAE.

The eggs of GYROCOTYLIDAE have a structure resembling that of Monogenea and Cestoda-PSEUDOPHYLLIDAE.

The larva emerging from an egg is characterized by the presence of a ciliated epithelium, 2 groups of head glands and 10 embryonic hooks (the latter are capable of moving). Judging by Ruszkowski's data, the larva does not have any traces of digestive system.

Whether it is justifiable to class GYROCOTYLIDAE among Cestoda is already quite clear from the above.

In fact, GYROCOTYLIDAE have the following characteristics in common with Cestoda: the absence of an intestine; in part the structure of the genital system, and, to some degree, the musculature. The following characteristics (which, as has been mentioned, have nothing in common with GYROCOTYLIDAE with respect to morphology and anatomy) are shared with AMPHILINIDAE: the absence of an intestine and a 10-hook larva (the so-called lycophore). Strictly speaking, only the last two characteristics made it necessary to class GYROCOTYLIDAE with Cestoidea-Cestodaria. However, the first characteristic merely indicates a great adaptation of the forms studied to endoparasitism. We know of many animals which have the same characteristic but are in no way related to Cestoda. As for the second characteristic, the 10-hook larva, as is known, is characteristic of the entire Monogenea group, and the larvae of GYROCOTYLIDAE differ from the larvae of the 2nd group of Monogenea only by the absence of the intestine.

On the other hand, the following very important characteristics are shared with Monogenea: 1) the presence of a posterior attachment disc in the adult forms, 2) the presence of two lateral excretory openings, 3) the structure of the nervous system, 4) the presence of a dorsal opening of the vaginal duct, etc.

As a result of the above analysis, we consider that the family GYROCOTYLIDAE should be excluded from Cestoidea-Cestodaria, as it was assigned to this group erroneously, and should be separated as an independent class which is somewhat closer to Monogenoidea than to Cestoidea, because within this family we, undoubtedly, observe a number of transitional features between Cestoda and Monogenea. These transitional features distinguish GYROCOTYLIDAE both from Monogenea and from Cestoda (see the system below).

The vaginal duct of GYROCOTYLIDAE opens near the edge of the body, in the vicinity of the male genital pore and opening of the uterus, but is dorsal and not ventral as these two openings are. Such an unusual arrangement of the vaginal duct openings never occurs in Cestoda, but quite frequently in Monogenea, as, for example, in MICROCOTYLIDAE.

The eggs of GYROCOTYLIDAE have a structure resembling that of Monogenea and Cestoda-PSEUDOPHYLLIDAE.

The larva emerging from an egg is characterized by the presence of a ciliated epithelium, 2 groups of head glands and 10 embryonic hooks (the latter are capable of moving). Judging by Ruszkowski's data, the larva does not have any traces of digestive system.

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V. Interrelationships of Cestoda and Monogenea and Janicki's Cercomere Theory

As can be clearly seen from the preceding section, we consider that Cestoda are connected in their origin with Monogenea. This is based on a number of considerations; first of all, the presence of a transitional group, and Janicki's cercomere theory somewhat modified by us. We consider that the primary larval stage of Cestoda was a freely floating larva provided at its posterior end with chitinoid hooks serving for attachment to the host's body. This larval stage is homologous to that of Monogenea, and, consequently, the chitinoid hooks of Cestoda and Monogenea are also mutually homologous. Later, due to the adaptation of Cestoda to endoparasitism, the physiological significance of the armature disappeared gradually, in all probability first in the adult forms (just as we observe it in a number of Monogenea, see above), and then in the larvae, so that at present the hooks of Cestoda's larvae are only phylogenetic "vestiges" of adaptative structures which had been extremely important at one time. It is interesting that the structure of these hooks of Cestoda larvae corresponds fully to that of Monogenea larvae. This is particularly remarkable if we take into consideration that such hook structure does not occur in any other groups of the animal kingdom.

The larvae preserving the primary features, i.e., having a ciliated covering, are encountered in Cestoda quite frequently. For example, we find them in Pseudophyllidea and in Tetrarhynchidea. In other orders of Cestoda, and partly in these two as well as the evolutionary process progresses considerably further, and the ciliated covering of the larvae disappears. However, they retain their special inner covering which, undoubtedly, is homologous to the ciliated epithelium of primary larvae. The onchosphere, i.e., the larva without the ciliated covering, as is known, has later a different fate in various groups of Cestoda. Further changes in the onchosphere can be seen in the included diagram [Fig. 3] which we took from Fuhrmann's work, modifying it somewhat. The diagram shows the development cycles of three major orders of Cestoda: Tetraphyllidea, Pseudophyllidea and Cyclophyllidea.

Janicki, in his cercomere theory, attached great importance to the tail outgrowths of the larvae of Cestoda, considering that these apophyses were homologous to the attachment disc of Monogenea. We can see from the diagram of Cestoda development that the caudal apophyses of the larvae of various orders vary greatly in their form and, finally, they disappear completely in the most specialized Cyclophyllidea. This fact, in our opinion, is not particularly important because it merely indicated a great adaptation of the latter forms to completely new conditions of existence, when many characteristics of more primitive larvae disappear.

However, we consider that all of the current disagreements regarding the homology of certain parts of the body of procercoid, cysticercus, and other Cestoda larvae are not of any fundamental significance for the cercomere theory (although the arguments are progressing chiefly in this direction). In our opinion, the posterior end of the onchosphere is, primarily, homologous to the attachment disc of Monogenea, and this is the one fact we must realize in order to accept Janicki's cercomere theory; this is done without paying any particular attention (naturally, only during the first stage of the analysis of his theory) to which of the subsequent larval stages of the Cestoda is an earlier one or which part of what larva is homologous to a cercomere, etc.

Thus, we shall repeat, the Cestoidea cercomere, in our opinion, is the posterior part of the onchosphere which is homologous to the attachment disc (posterior end of the larva) of Monogenea.

We shall say a few words regarding the homology of the hooks of the onchosphere and the hooks of the attachment disc of Monogenea. There is no doubt that the hooks of the onchosphere are homologous to the lateral hooks of Monogenea, and when we pointed out the similarity in the form of these structures in both groups, we had this interrelationship in mind. Of course, it should be mentioned that the comparison of the onchosphere hooks with the medial hooks of Nitzschia made by Janicki was erroneous, and resulted because he was excessively impressed by the coincidence in the number of the onchosphere hooks and the number of the medial hooks of Nitzschia.

In some Cestoda larvae, the developing tail apophysis has no embryonic hooks which remain in the body of the larva itself. This fact, which is sometimes used as an argument against homologizing such an outgrowth to a cercomere, is very interesting because it shows the process of the initial development of hooks within both groups which are being compared. The point is that, in Monogenea, the lateral hooks also can start developing somewhat above the posterior end of the body, and only later the developed hooks "descend" to the attachment disc. As we see, this lowering" is also observed in some Cestoda, although it no longer has physiological significance (the latter is probable, but has not been proven) and in some of them the "descent" does not occur in those where the onchosphere hooks definitely have no significance in the life of the subsequent larva.

Without going into details, we shall mention that it is possible to compare the genital systems of Monogenea and Cestoda, although the difference between the genital systems of these two groups is very considerable. When comparing these systems, we must consider the vaginal ducts of Monogenea and Cestoda to be equivalent. The characteristic feature of Cestoda -- the presence of a common opening for the male genital system and the vaginal duct -- does not occur in Monogenea.

However, in very many forms, particularly among Oligonchoinea, we encounter the male genital opening and the opening (openings) of the vaginal duct situated extremely close to each other, and in some representatives of the same subclass of Monogenea the opening of the uterus is not connected with the male genital pore. Such relationships(as in GYROCOTYLIDAE, see above) make it possible to assume subsequent changes in the interrelations of the ducts in various directions, particularly in the direction of the interrelations occurring in Cestoda. The situation is more complicated in the case of the male copulatory organ represented by a penis in Monogenea, and by a cirrus in Cestoda. However, it should be mentioned that the presence of a penis is a sign of a more primitive structure, which is encountered among Cestoidea in Cestodaria-Amphilinidea, therefore this characteristic cannot be a fundamental distinction of Cestoda from Monogenea.

However, it should be noted that a very detailed comparison of the structure of the genital systems of the two classes is even unjustifiable, because it is quite natural to have differences in the structure of a system of organs in such highly-differentiated groups as classes (it would be particularly obvious if we would be comparing classes of Arthropoda or Vertebrata).

Let us now say a few words regarding the position of AMPHILINIDAE in the system. This family is, undoubtedly, an extremely isolated group from which it is impossible to derive another group (as was done, for example, by Janicki, who considered some AMPHILINIDAE as being transitional forms between Cestoda and Trematoda). In agreement with many authors, we consider that this family consists of Cestoda larvae which became sexually mature in the process of their evolution. This is also confirmed by the data on the development of Amphilina in which we see the presence of only one larval stage, the procercoid, while it itself (as well as all other AMPHILINIDAE) lives as a pleurocercoid in the body cavity of its host. However, we believe, as will be seen later, that Amphilinidae originated from tapeworms which are not equivalent to the modern ones, so that their isolation as an independent subclass, Cestoidea, is, in our opinion, quite justifiable, and it would probably be more correct to isolate this group as an independent class. However, the latter is based only on indirect considerations which, naturally, we cannot rightfully use.

Concluding this section, let us sum up what has been said above. Our principal conclusion is that Cestoda originated from Monogenea-like ancestors and that the intermediate group was GYROCOTYLIDAE.

Janicki's cercomere theory quite justly stresses the phylogenetic affinity of Monogenea and Cestoda, but attempted, absolutely incorrectly, to include digenetic trematodes of an entirely different origin into the group of cercomeromorphic Platoda. The inclusion of this group contributed to the development of a very strong critical trend which

negated the theory itself because of the incorrect part of it. If we reject this erroneous portion and not interest ourselves in some of the disputable details, we shall obtain a theory which is extremely fruitful in understaiding the problems of the phylogenesis of Platoda. In all probability, attempts will be made even now to disprove it. But it seems to us, it will be impossible to disprove it in its new modified form by using the latest data.

We shall leave it to specialists on tapeworms to judge the correctness of Fuhrmann's viewpoint regarding the evolutionary lines within Cestoda. However, it seems to us that he was completely wrong in his thesis that from forms having 2 bothridia it is difficult to derive forms with 4 bothridia or 4 suckers (while the reverse process, in his opinion, progresses sufficiently easily). It should be assumed that the primary Cestoda had two head adhesive organs, so that in this respect there are certain advantages in the viewpoint according to which the most primitive ones are PSEUDOPHYLLIDAE and not Tetraphyllidea, as Fuhrmann believes. The reasons for which we believe that the primary Cestoda could have had two cephalic attachment organs are clear from the above discussions and do not need to be repeated.

VI. General Picture of the Evolution of Parasitic Flatworms

We view the general picture of the evolution of parasitic flatworms in the following manner. Two completely independent branches come from Rhabdocoela, the first of which is represented by the class Trematoda (in its new meaning), and the second is the initial one for the entire superclass Cercomeromorphae.

The beginning of the branch Cercomeromorphae is characterized in all probability by the appearance of Monogenea-like worms leading an ectoparasitic mode of life, possibly even capable of leaving their host for a while, similar to present-day leeches. These hypothetical ancestors of Cercomeromorphae were characterized by the presence of chitinoid hooks on the attachment disc. In all probability, the number of these hooks was quite considerable.

The evolution of the group from these forms progressed extremely rapidly along two main directions: the first was directed toward adaptation to ectoparasitism which gave rise to, first of all, Monogenea, while the second was toward endoparasitism and gave rise to Cestoidea. It should be mentioned that the first direction which gave rise to Monogenea undoubtedly appeared earlier than the second. A part of these forms was also moving toward endoparasitism, but unlike the Cestoidea, these forms retained the posterior attachment organ in their adult state. In all probability, these forms gradually became extinct and only a few of them reached us in the form of the representatives of the family GYROCOTYLIDAE (with a small infrequent number of species and genera and a very broad geographic distribution).

The line Cestoidea at first evidently had larvae with a greater number of chitinoid hooks than the modern forms; it is from these more ancient Cestoidea that Cestodaria originated. In all likelihood, the final separation of the latter took place during the extinction of the true primary Cestodaria which had two intermediate hosts and changed into tapeworms with a greater or lesser number of segments in the final host. It is tempting to think that the extinction of these "Procestodaria" took place during the period of extinction of ancient reptiles, i.e., most probably not any earlier than the Jurassic period. This viewpoint has been treated with sufficient detail by Janicki and seems very probable to us.

The line of the true Cestoda became separated, undoubtedly, somewhat later than Procestodaria; probably, however, the development of these two lines progressed in parallel for a long time.

The phylogenetic scheme of parasitic flatworms proposed by us does not claim any historical accuracy at all - this is only a scheme in which geological periods are shown in order to give some idea of the time of evolution. We consider that the appearance of Trematoda coincided in time with the appearance of vertebrates, while the appearance of primary Cercomeromorphae was, possibly, somewhat earlier, although the separation of all groups which have reached the modern period took place in exactly the same way during the time of appearance of the first vertebrates, i.e., fish.

Let us mention that it is completely unclear to us at what time the intermediate hosts of Cestoidea and Trematoda appeared and how this process progressed. However, if Janicki's viewpoint regarding AMPHILINIDAE is correct (and evidently, it is so), the process of the formation of a cycle with two intermediate hosts of Cestoidea ended completely between the Silurian and Jurassic periods. However, at the present time it is not our goal to study the origin of the phenomenon of intermediate hosts, because this phenomenon does not play a significant role in the problems which are of interest to us.

As can be seen from our general scheme of the evolution of parasitic flatworms, we have made a number of taxonomic regroupings. Consequently, we are concluding this section by explaining the system suggested by us and indicating after the diagnosis of each group to what it corresponds according to the system generally accepted at the present time. Groups which were not changed by us are shown without diagnosis.

Cladus Plathelminthes Vogt.
Class Turbellaria Ehrenberg.
Retained without changes.
Class Trematoda.

Diagnosis (partly according to Fuhrmann): Trematoda are mostly colorless endoparasites, less frequently ectoparasites. The body is usually flattened, less frequently cylindrical. The cuticle may be armed with spines or scales. The attachment apparatus consists of an oral sucker, and a ventral sucker, or a posterior sucker, arranged along the central line of the body; one of the suckers, or both, may be rudimentary or may even disappear. The mouth opening is terminal, or subterminal, or in the middle of the ventral surface of the body. A phraynx is usually present. The intestine is usually bifurcated, less frequently it is sacciform or branching, quite often the crura of the intestine merge with each other posteriorly. Only as an exception, are there one or two anal apertures. One excretory opening is at the posterior end of the body. They are hermaphrodites, less frequently dioecious. Genital pores are arranged variously. Usually, there is one opening for the uterus and the male genital system (genital cloaca). Laurer's canal is often present. There are two testes, less frequently only one or many. The uterus usually has a large number of eggs. Development occurs with alternation of generations and hosts (exception: Aspidogaster?). The presence of parthenogenesis during development is a chracteristic feature. Sexually mature worms parasitize, with rare exceptions, vertebrates.

This class corresponds to the order Digenea according to modern taxonomy.

Superclass Cercomeromorphae (Janicki) Bychowsky.

Diagnosis: Plathelminthes possessing primary larvae equipped with embryonic hooks at the posterior end which are ectoparasites or endoparasites in the adult state.

Group (subsuperclass) Monogenoidei n. scl.

Diagnosis: Cercomeromorphae having an attachment apparatus at the posterior end of the body in their adult state.

1st Class. Monogenoidea (Beneden) Bychowsky (syn. Polystomoidea Baer).

Diagnosis: Monogenetic trematodes which are ectoparasites and, only as an exception, endoparasitic. The body is colorless and more or less flattened in the dorsoventral direction. The adhesive apparatus is well developed and is situated at the posterior end of the body. It is represented by a disc with organs of adhesion on it in the form of hooks, or suckers, or valves. Sometimes the disc itself changes into a sucker which is often subdivided by septa into separate sections. The mouth opening is terminal or subterminal. The intestine consists of two crura which often form branches and commissures which frequently fuse at the posterior end of the body. Less frequently the intestine is in the form of one crus. There are two excretory openings which are

placed in the anterior half of the body laterally, on either the ventral side or on the dorsal side. They are hermaphrodites. The copulatory organ is either equipped with chitinoid parts or not. There are one or two testes, or quite often a large number of them. The uterus is usually short and contains only one egg. Development is direct, without alternation of generations and hosts; most frequently with metamorphosis. Parasites of cold-blooded vertebrates, as an exception on parasitic crustaceans, cephalopods and aquatic mammals.

This class corresponds to the order Monogenea according to modern taxonomy.

2nd Class. Gyrocotyloidea n. cl.

Diagnosis (after Fuhrmann): Monogenoidei whose adhesive disc is changed either into a funnel with a greatly plicated edge or into a cylindrical tube. The anterior end has a rather muscular sucker. There is no digestive system. The reticular excretory system opens by two lateral apertures on the ventral side of the body at the level of the genital pores. The opening of the uterus lies ventrally and medially, the male genital pore is to the side of the uterine opening, and the opening of the vaginal duct is situated dorsally opposite the male genital pore. The copulatory apparatus is in the form of a conical penis situated in the male genital cloaca. Testes are numerous. The ovary is follicular. The yolk glands are well developed. The uterus is very convoluted with a large number of eggs. Development is unknown, probably direct and without alternation of hosts. The larva is free-swimming, without an intestine. Parasites of Holocephala.

This group corresponds to the order Gyrocotylidea according to the modern taxonomy.

Group (subsuperclass) Cestoidei n. sscl.

Diagnosis: Cercomeromorphae which have an attachment apparatus at the anterior end of the body in their adult state.

Class Cestoidea Rudolphi.

Diagnosis: Tapeworms which are always endoparasites; in the sexually mature state they live in the intestines, less frequently in the body cavity of vertebrates (exception: Archigetes living in the body cavity of fresh-water Oligochaeta). The attachment apparatus is usually well developed and is situated at the anterior end of the body. A digestive system is completely absent both in the adult animals and in all larval stages. The excretory system opens by one aperture at the posterior end of the body. Hermaphrodites, as an exception dioecious. The copulatory organ, as a rule, is in the form of a cirrus; a penis occurs as an exception. Testes are numerous. The

uterus is usually well developed and contains a large number of eggs. Development progresses with alternation of stages and hosts. Absence of parthenogenesis is a characteristic feature; quite often, asexual reproduction (gemmation) occurs in larval stages.

Subclass Cestodaria Monticelli.

Diagnosis (after Fuhrmann): Cestoidea of a foliate or ribbon-like shape, without a clearly developed head, and with a proboscis upon which a large number of special head glands open. The nervous system consists of two lateral trunks interconnected by commissures anteriorly and posteriorly. The excretory system is in the form of a network of vessels; it opens externally by one aperture at the posterior end of the body. The end cells of the excretory system have a large number of clusters of cilia. Seminal vesicles are very numerous. There is a penis with a propulsion apparatus in back of it and a pars prostatica. The ovary, without an egg reservoir, lies near the posterior end of the body; it has smooth edges and is more or less palmate. The yolk glands are very extended and usually narrow. The vaginal duct is either single or double, and opens externally near the posterior end of the body. The uterus consists of two ascending branches and one descending branch; it opens near the proboscis at the anterior end of the body. Parasites in body cavities of fish, particularly in ganoids.

This subclass corresponds to the order Amphilinidae Poche according to current taxonomy.

Subclass Cestoda Monticelli.

Retained without changes.

CONCLUSION

The opinions presented in this report on the interrelationships of ontogeny and phylogeny of parasitic flatworms, and the system based on them are, on the one hand, the results of our nearly ten-year long studies of monogenetic and digenetic trematodes, and, on the other, the results of studying the works of the prematurely deceased and most talented scholar Janicki, particularly his works on the cercomere theory.

We believe that this theory will serve for a long time as the most fruitful source for the development of studies in the phylogeny of parasitic flat worms.

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Discussion of the Report of B.E. Bychowsky

Professor Beklemishev remarks that he subscribes to the general scheme presented by the speaker. There is no doubt about the origin of parasitic flat worms from Rhabdocoela and more precisely, from Dallyellidae-Graffillidae. As for Trematoda, it is very possible that originally these animals parasitized molluscs. Monogenetic trematodes, undoubtedly, have not been analyzed well until now, and it is difficult to express an opinion about them. However, their genital apparatus is close to the rhabdocoel type. It is possible that the structure of the pharynx may yield a lot of information on the issue, because this character is very important in the case of Turbellaria. With regard to tapeworms, it is necessary to say that the structure of the female genital apparatus indicates their sharp distinction from Digenea and the majority of Monogenea. Therefore, there is no doubt that we cannot derive Cestoda from a Digenea type.

Professor Dogiel points out that the report is a result of many years of research by the speaker, and that the material obtained by him makes it necessary to revise radically the taxonomic system of a very large group. This involves the creation of new classes, subclasses, etc. If, for a comparison, we consider the taxonomy of arthropods, we shall see how extensive the problems here are involved. Besides the general context, there are many very interesting points, as, for instance, determination of the position of Gyrocotyle in the system.

The entire work contains a lot of good, substantiated material. It is believed that this report will greatly stabilize the problem of the interrelationship between parasitic flatworms and free-living worms. We can fully subscribe to the speaker's opinions. It is believed that this taxonomic system will become established.

Professor Pavlovsky remarks that the systems of parasitic worms which have existed until this time were developed on the basis of comparative anatomy, because the latter yields the largest number of starting points for the purposes of taxonomy. But the speaker takes the data of ontogenesis and makes the most of the significance of the phylogeny of larval forms. This is fruitful and brings his system closer to a natural system, because this also involves the utilization of the data on the historical development of groups of animals. In the future, experimental studies will also be needed.

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